

THE ROLE OF POD CORN IN THE ORIGIN AND EVOLUTION OF MAIZE

PAUL C. MANGELSDORF

Botanical Museum, Harvard University, Cambridge, Mass.

THE POD-CORN HYPOTHESIS

The hypothesis which holds that cultivated maize has been derived from a wild form of pod corn at one time indigenous to the lowlands of South America is at once the oldest and among the youngest of the various propositions which have been developed to explain the origin of this unique New World cereal. More than a century ago the French naturalist, Saint-Hilaire (1829), described as a new variety *Zea Maïs var. tunicata*, a peculiar type of maize sent to him from Brazil in which the grains were covered by the glumes. He concluded that this was the natural state of maize and that South America (Paraguay) was its native home. Virtually all students of maize since Saint-Hilaire have given serious attention to pod corn, have recognized its primitive characteristics, and have either accepted it as the ancestral form, or, for a variety of reasons, have dismissed it from this role. Their viewpoints and conclusions are reviewed and discussed in detail by Mangelsdorf and Reeves (1939). Here it will suffice to set forth the principal reasons given by various students who dismissed pod corn as the ancestral form of maize: (1) it does not breed true; (2) it apparently arises spontaneously in cultures of normal maize; (3) it is frequently monstrous; (4) it differs from normal maize primarily by a single gene; (5) the hypothesis that teosinte is the ancestral form of maize is a more plausible one.

Of the five reasons given for rejecting the pod-corn hypothesis the last is particularly important, for, once the close relationship of maize and teosinte was widely recognized, the pod-corn hypothesis was relegated to a distinctly secondary role. Only recently has it again been brought into prominence by Mangelsdorf and Reeves (1939) who, on the basis of experimental evidence, concluded that teosinte, far from being the progenitor of maize, is instead the progeny of the hybridization of maize and *Tripsacum*. Having dismissed teosinte as the ancestral form of maize, they turned to the earlier pod-corn hypothesis as the only plausible alternative.

The present paper is concerned not with the entire problem of the origin of maize but primarily with the pod-corn hypothesis, and particularly with a mass of new experimental evidence and new observations accumulated during the past ten years which have a bearing upon the problem of the role of pod corn in the origin and evolution of maize. Data previously published are included only to the extent that they are needed in presenting a complete picture; and the extensive literature on pod corn is reviewed only to the extent of providing an adequate background for the present discussion. For more detailed reviews of the literature on pod corn and for earlier data the reader is referred to Sturtevant (1899), Weatherwax (1935), and Mangelsdorf and Reeves (1939).

THE HISTORY AND DISTRIBUTION OF POD CORN

Early History References.—

Since the early history of pod corn has been adequately treated by Sturtevant (1899) there is no necessity for including a detailed review here, and only those references which appear to be highly significant to the pod-corn hypothesis are mentioned. The four references to pod corn which appeared in the first third of the nineteenth century seem to me to be especially important. These are: Azara (1809), Dobrizhoffer (1822), Saint-Hilaire (1829), and Bonafous (1836). All deal with pod corn in South America and three of them with pod corn in Paraguay. Two of them, significantly, speak of pod corn as *bisingallo* or *pisingallo*, words undoubtedly related to the modern words *pisingallo*, *passankalla*, *pisincho*, *pinga*, and *piksenkella* which Parodi (1935) and Granado (1931) have listed as being used in South America for varieties of pop corn. Mangelsdorf and Reeves (1939) have pointed out that the use of the word *pisingallo* in connection with pod corn in the nineteenth century and the use of its derivatives in connection with pop corn in the twentieth century is quite consistent with the conclusion first clearly stated by Sturtevant (1894) that primitive corn was both a *pod* corn and a *pop* corn.

Experimental Verification of an Historical Reference.—

Especially significant to the pod-corn hypothesis and of particular interest in connection with the conclusion that primitive corn was both a pod corn and a pop corn is Azara's (1809) description of the fourth kind of maize which he encountered in Paraguay. Since this description has been quoted in full elsewhere (Mangelsdorf and Reeves, 1939), it need only be said here that Azara described a variety of maize bearing covered seeds in the tassel. This corn was utilized by heating the tassel in oil, whereupon the kernels, still attached to the tassel, exploded to produce, in Azara's own words, a "superb bouquet capable of adorning at night the head of a lady."

By crossing pod corn with pop corn and by backcrossing the hybrid to pop corn for several generations it has been possible to produce a corn which is both pod corn and pop corn and which dipped in hot oil behaves precisely like the fourth variety described by Azara. This simple experiment is not proof that Azara was describing a primitive form of corn. It does prove, however, that what he described *could* have been a pod-pop corn. And since the third variety of corn which Azara described was obviously pod corn there is little doubt in my mind that Azara has given us a description, remarkably picturesque and vivid, of a primitive homozygous pod corn whose seeds were not only covered but also were small, hard, and capable of popping.

Present Occurrence of Pod Corn.—

During the second two-thirds of the nineteenth century, pod corn was repeatedly reported from various parts of North America. It is difficult to determine the significance of some of those reports since pod corn came to be regarded as an interesting curiosity and was actually sold as a novelty by seedsmen (Sturtevant, 1899). Even today it is still passed from person to person and grown as a curiosity so that its occasional spontaneous appearance in open-pollinated fields is of no significance from the standpoint of proving recurrent mutation.

Much more significant, I think, is the possession of pod corn by native peoples. Parker (1910) stated that pod corn was among the varieties grown by the Mohawk and Iroquois Indians and that by the latter it was regarded as sacred. Pod corn occurs in Mexico. I have never encountered pod corn in the field in Mexico but Ing. Eduardo Limón and Ing. Edmundo Taboada of the Dirección de Agricultura in Mexico both have told me that pod corn exists in Mexico, and it has been reported by Khankhoje (1930). There are also ears of pod corn of uncertain origin on display in the local museum near the pyramid of Teotihuacán.

Pod corn is widely known in South America. Contrary to Cook's conclusion (cf. Collins, 1917) that pod corn is unknown in Peru and that there are no words for it in the Quichua vocabulary it can now be said that pod corn, although not common, is well known not only in Peru but also in Bolivia, Ecuador, and Colombia, and that there is a well-recognized term *paca sara* meaning "hidden maize" to describe it. Cutler (1944) has made several collections of pod corn in Bolivia and has made the interesting suggestion that it has been kept in existence and distributed far and wide by the Callahuayo itinerant medicine men. Pod corn of several distinct types, one of which is illustrated in pl. 43A, has been sent to me by Professor Cesar Vargas from Peru. Dr. Arthur G. Kevorkian has told me that pod corn is grown for its magical properties in Zamora, Ecuador, and Dr. Fernando Villamil of the Agricultural Experiment Station at Palmira, Colombia, has informed me that pod corn is well-known in several localities in Colombia. Brieger (1945) has described a form of pod corn from Brazil.

Pod Corn in Prehistoric Maize.—

There is at least one authentic specimen of prehistoric pod corn in the Museum of Northern Arizona at Flagstaff, mentioned by Cutler (1944). The ears of pod corn in the Museum at Teotihuacán in Mexico, already mentioned above, are said to be prehistoric but the evidence is not conclusive. In addition, there are a number of prehistoric ceramic replicas of corn ears which *may* represent pod corn. One of the most convincing is the specimen in the Peabody Museum of Yale University illustrated by Mangelsdorf and Reeves in their fig. 92. Another from the same museum which may be, but certainly is not necessarily, pod corn is illustrated in their fig. 15. Several of the representations of maize on early Peruvian pottery at the American Museum of Natural History show at least external resemblances to pod corn (Mangelsdorf and Reeves, fig. 16). Finally there is a specimen in

the Museum of the University of Pennsylvania which might easily be taken as representing pod corn.

The probability that some or all of these prehistoric specimens were intended to represent pod corn has been enormously increased by the discovery, described elsewhere in this paper, that many of the actual ears of prehistoric corn still in existence are a weak form of pod corn.

THE NATURE OF POD CORN

Genetic Nature.—

Genetically, pod corn, or "tunicate" as it is commonly known among maize geneticists, is the phenotypic expression of a single gene *Tu* located in the long arm of chromosome 4. The *Tu* gene is strongly but not wholly dominant. It always manifests itself in the heterozygous condition but two doses of the gene usually produce a greater effect than one. The *Tu* gene is responsible for producing the principal effects which are characteristic of pod corn, but the degree to which these effects manifest themselves is strongly influenced by modifier factors which are undoubtedly distributed over several chromosomes and probably over the entire chromosome complex.

Morphological Nature.—

The expression of the *Tu* gene varies with the environment and with the background of modifying factors, but the gene is one which usually has manifold effects. Those most commonly recognized are described below:

Glumes:—The principal characteristic of pod corn is that the glumes, which in ordinary corn are reduced to inconspicuous bracts, are completely functional and, as in other cereals, enclose the caryopsis. There is enormous variation in the degree to which the glumes develop. In some ears they are monstrous; in others they scarcely enclose the grain. On any one ear of pod corn the glumes are usually more strongly developed at the base of the ear than at the tip. The reason for this is not known.

The *Tu* gene affects not only the glumes of the pistillate spikelets but also the glumes of the staminate spikelets in the tassel. This second effect is less noticeable than the first since the staminate spikelets already normally have glumes completely enclosing the floral structures. Nevertheless, it is usually possible to distinguish tunicate or heterozygous tunicate plants from non-tunicate plants in the same family by the size of the glumes on the staminate spikelets.

Another characteristic of the glumes of pod corn is that they are membranaceous or papery rather than indurated or horny. In this respect pod corn differs not only from teosinte and *Tripsacum*, the closest relatives of maize, but also from most varieties of *Coix* and of *Sorghum*. Membranaceous glumes are not, however, unique to pod corn since they are characteristic of many grasses.

Staminate and Pistillate Spikelets:—The second most conspicuous effect of the *Tu* gene is evident in the terminal inflorescence or tassel. This structure, normally

wholly staminate in the majority of modern corn varieties, becomes partly pistillate in the presence of the *Tu* gene, sometimes in plants heterozygous for the gene, almost always in plants homozygous for it.

The transformation of a staminate inflorescence to a partly pistillate one may occur in various ways. Dissection and examination of several thousand florets in the tassels of *TuTu* and *Tutu* plants have led to the following observations:

1. Florets on a mixed inflorescence may be: (a) functionally pistillate; (b) functionally staminate; (c) perfect; (d) functionally pistillate with visible but non-functional anthers; and (e) abortively staminate.

2. Pistillate or perfect florets are most common in the lower spikelets on the tassel branch, but are not confined to them.

3. If both florets in a single spikelet develop, both may be staminate (common), both pistillate (rare), the upper pistillate and the lower staminate (rare), or the upper perfect and the lower pistillate (common).

4. If only one floret in a spikelet is pistillate, it is invariably the upper.

5. If only one floret in a spikelet is perfect, it is invariably the upper.

6. When pistillate, perfect-flowered and staminate spikelets all are found on the same branch, the pistillate are likely to occur below, the staminate above, and the perfect-flowered between.

The degree to which the tassels of pod corn become pistillate, like the development of the glumes, varies with the environment and the genetic background. There is, however, a strong correlation between glume development and sex-reversal in the tassel. Heterozygous tunicate plants which are strongly pistillate in the tassel are almost certain to have prominent development of glumes on the ear, when there is an ear.

If the terminal inflorescence, or tassel, is strongly pistillate, then the lateral inflorescence, or ear, is likely to be suppressed. This is probably a simple matter of the amount of plant nutrients available, and the fact that the terminal inflorescence apparently has priority in its requirements. It is usually possible to induce the formation of an ear in a tunicate plant which would otherwise be earless by removing the tassel soon after it emerges.

Secondary Pistillate Florets:—The tunicate condition is often, but by no means always, accompanied by the development of secondary pistillate florets. This may occur either in the tassel or in the ear. An example of the latter is illustrated in pl. 45C. This condition, which is a genetic one in the sweet corn variety, Country Gentleman, is in tunicate maize undoubtedly the consequence, at least in part, of the release which the tunicate condition provides from compaction and pressure. This is suggested by ears which have elongated beyond their husks. On such ears, spikelets with the lower floret developed occur almost invariably in the region not compressed by the husks.

Branching of the Ear:—In some stocks, notably in my crosses of pod corn with the Guarany maize of Paraguay, the tunicate condition is often accompanied

by basal branching of the ear. Since the basal branches are two-ranked, they contribute toward producing a structure which, except for the fact that it is pistillate rather than staminate, is the exact counterpart of the tassel, a polystichous central spike with distichous basal branches. An ear of this type is shown in pl. 44.

Basal branching of the ear, like the development of secondary florets, is probably in part a response to release from compaction.

Elongation of the Rachis:—One of the most conspicuous effects of the tunicate gene, and one whose consequences have already been described in part, is a release of the strong compaction characteristic of the normal modern ear of corn, which, as I have pointed out elsewhere (1945), is a strongly compacted structure. The extent to which compaction is released, like other effects of the *Tu* gene, varies with the environment and with the genetic background. In some stocks, again notably in crosses of pod corn by Guarany maize, the ear grows far beyond the husks and becomes so lax that its true nature is clearly revealed (pl. 42). The rachis is slender and fragile like the rachises of other cereals. The paired nature of the pistillate spikelets, obscured in many modern varieties of maize, is readily apparent, and in some cases the sessile and pedicellate members of the pair are distinguishable. In some ears of pod corn the whorled phyllotaxy of the inflorescence is also clearly revealed.

Elongation of the "Shank":—Also, sometimes, but by no means always, accompanying the tunicate condition is an elongation of the stalk, commonly known as the "shank," upon which the ear is borne. Here again environment and modifying factors play a part. The most striking example of this elongation which I have encountered occurred in a plant of Guarany pod corn which bore three ears on its main stalk and one ear on each of its three tillers. The ears on the tiller stalks were normal with contracted shanks and normal husk covering, but the three ears on the main stalk all had elongated shanks bearing more or less normal leaves instead of husks at the nodes, and terminating in naked or partly naked ears. This plant is an excellent demonstration of the widely accepted conclusion that the ear of maize is the terminal inflorescence of a lateral branch which has become drastically contracted and that the husks are leaf sheaths arising from each node which have largely lost their leaf blades and which because of the contraction of the branch have become strongly overlapping. This plant also demonstrates that all of these profound changes can occur spontaneously and almost as a single step. In this instance the tunicate gene has apparently brought the plant to a threshold where slight differences in the environment (the kind of difference in environment which exists between the main stalk and the tillers) may have drastic and dramatic effects.

Other Effects: How many other effects the *Tu* gene produces remains to be determined. Preliminary investigations by Prat (reported in a conversation)

indicate that the epidermal characteristics of tunicate maize are different from those of non-tunicate maize and are of a category which he regards as primitive for the grasses. There is little doubt that still other differences between tunicate and non-tunicate maize will be found when more intensive morphological studies have been made.

Effect of Tu on Teosinte.—

Brieger (1944) is of the opinion that the spikes resulting from crossing teosinte and pod corn followed by backcrossing to teosinte provide an experimental reconstruction of wild corn. I do not share that opinion. It is clear, however, that such crosses can shed light not only on the morphological nature of teosinte but also on that of pod corn.

Certain effects of pod corn are emphasized and clearly revealed when the *Tu* gene is introduced into varieties of teosinte by hybridization of pod corn and teosinte, followed by repeated backcrossing to teosinte. Fruits of tunicate teosinte compared with fruits of normal teosinte are illustrated in pl. 46. In normal teosinte the fruit case comprises an indurated glume of restricted proportions plus an indurated rachis segment which internally is concave and partly surrounds the caryopsis. In tunicate teosinte the caryopsis is completely enclosed by prominent, membranaceous glumes, and the rachis segment becomes nothing more than an appendage¹, playing no part in enclosing the caryopsis. These two fruit cases, so different that if encountered in nature they would undoubtedly be assigned to different species if not to different genera, are the products of the two genes *tu* and *Tu*. The segregation of the two types is approximately 1:1 in backcrosses of the heterozygote to the recessive. This fact may be of considerable significance in the study of the world's corn varieties. It is almost certain that varieties of corn originating from a strong introgression of *Tripsacum* into maize, either directly or through contamination of maize by teosinte, would have quite a different cob anatomy from those originating directly from any kind of tunicate maize. The former, which we may call "tripsacoid," would be a compound structure made up of individual units fundamentally like the fruit case of normal teosinte, but modified by crowding and pressure. Such a cob would be expected to have a thick, stiff, and indurated rachis with distinct rachis cavities from which arise spikelets whose outer glume is reduced to an indurated bract. On the other hand, a cob derived from a tunicate or weak tunicate maize, which we may call "tunicoid," would be expected, since it is made up of units fundamentally like the fruit case of tunicate teosinte, to have a slender, flexible, or fragile rachis, with the spikelets arising from its surfaces partly enclosed in membranaceous glumes.

There is no doubt that maize varieties possessing these two kinds of cobs exist. And since stocks with the indurated rachis and glumes of teosinte can be produced by controlled introgression of teosinte into maize there is little doubt that some

¹None of the fruits of tunicate teosinte in my cultures resemble those illustrated by Brieger in which the rachis remains intact and separation occurs at the base of the grain.

maize varieties of this type have arisen through such introgression. On the other hand, since the two types of teosinte described above differ primarily by a single gene it is possible that a tripsacoid type of maize ear, or something approaching it, can result from a simple mutation of *Tu* or one of its alleles to *tu* in a tunicoid type.

Most of this is obviously highly speculative and is included here only because it suggests some of the problems to which pod corn seems to hold at least one of the keys.

The Primitive Nature of Pod Corn.—

Many, if not all, of the effects of the *Tu* gene result in conditions which have been recognized as primitive by students of maize and its relatives. That wild corn must have had its grains enclosed in glumes has been noted by virtually all students of maize. That the ear is the terminal inflorescence of a drastically contracted lateral branch is widely accepted. That the husks are overlapping leaf sheaths minus the leaf blades is scarcely a matter for dispute. That the ear is the counterpart of the central spike of the tassel and is similar to a tassel minus its basal branches has been pointed out by several writers. Hence, in all of these features the *Tu* gene has the *tendency* to restore a condition which was undoubtedly characteristic of primitive maize.

It is possible, but not certain, that the tendency of tunicate maize to develop perfect-flowered spikelets and secondary pistillate florets also represents a reversion to a more primitive condition. It is generally recognized that the remote ancestor of maize and its relatives must have been perfect-flowered. But since *Tripsacum* and teosinte, the closest relatives of maize, are monoecious rather than perfect-flowered, I am inclined to believe that the occurrence of perfect-flowered spikelets in the tassels of tunicate maize represents a transition from a wholly staminate condition to one in which, as in *Tripsacum*, there are staminate and pistillate spikelets borne more or less separately on the same branches. The evidence for this, in so far as there is any evidence in tunicate maize, lies in the fact that inflorescences which are wholly perfect-flowered are never found. Perfect florets occur only in mixed inflorescences and are often found between a part of the branch bearing mainly pistillate florets and one bearing mainly staminate florets.

The significance of secondary pistillate florets in pod corn is even less clear. As already suggested, they may be nothing more than the consequence of a release from compaction. On the other hand, since the development of both florets is undoubtedly primitive in the grasses and since there are varieties of maize such as Country Gentleman in which the development of both florets is the rule rather than the exception, I suspect, although I certainly cannot prove, that the development of both florets in pod corn represents a tendency to revert to a condition characteristic of primitive maize. In this connection it is of interest to note that Dr. Cutler collected in the same village in Bolivia ears of tunicate maize and ears of maize which were not only branched but also bore secondary pistillate florets.

Leaving open the question of the significance of perfect florets and secondary pistillate florets in pod corn it is still obvious that the *Tu* gene is one which has a tendency to restore, not only the universally recognized primitive characteristic of glume-covered seeds, but an entire complex of primitive characteristics as well.

NEW GENETIC EVIDENCE ON POD CORN

True-breeding Pod Corn.—

One of the recurrent objections to the pod-corn hypothesis is that pod corn does not breed true. Homozygous pod corn, when it occurs in the cultures of the geneticist, is usually pollen-sterile and hence incapable of reproducing itself. It has already been pointed out (Mangelsdorf and Reeves, 1939) that this objection is not necessarily valid, since, if pod corn were the primitive type, then the *Tu* gene of today is a relict "wild" gene superimposed upon a genetic background frequently lacking in the background of modifiers which once kept the character under control. In the absence of these controlling modifiers the tunicate character would be expected to result frequently in monstrous development of the glumes accompanied by partial or complete sterility. This sterility is sometimes structural and sometimes probably physiological. Structural sterility exists when functional anthers are formed which, because of the sheer massiveness of the glumes surrounding them, are incapable of becoming exerted. Sterility thought to be of a physiological nature occurs when the glumes are so monstrous and demand so much energy in their development that, as a result, both male and female reproductive organs are abortive. In any case, there is great variation in the development of the tunicate character, and, as I previously pointed out (1947), there seemed to be a possibility of producing a completely fertile form of pod corn either by (a) selecting for restraining modifying factors or (b) substituting for the modifier complex of present-day pod corn a more ancient complex obtained from a primitive variety.

In a previous paper (1947) I reported that an experiment involving selection for minus modifiers of pod corn had been brought to a successful conclusion. I must now modify that statement, for although I did succeed in producing a number of true-breeding lines of pod corn by selection for minus modifiers, the extreme form which I described and illustrated has since proved to be the product not only of the accumulation of minus modifiers but also of a new allele at the *Tu-tu* locus. This new form of pod corn is described in some detail later in this paper. Homozygous forms of pod corn involving the original allele have much more prominent glumes than the new form illustrated in my previous paper (1947).

The other experiment previously reported, which sought to develop a true-breeding pod corn by introducing the modifier complex of a primitive variety, has not yet been completed. There is no doubt that the Guarany maize from Paraguay which was used in this experiment possesses modifiers capable of restraining the tunicate character. Furthermore, homozygous tunicate plants derived from

this experiment which are both male-fertile and female-fertile have been observed. There is little doubt, therefore, that a homozygous true-breeding form of pod corn will be produced in due time as a consequence of introducing modifiers of the tunicate character from a primitive variety.

Alleles of Pod Corn.—

As already mentioned, the attempt to produce a true-breeding pod corn through selection for minus modifiers resulted in the discovery of a new allele of *Tu*. The circumstances were as follows: in 1942, in a population derived from self-pollinating a *Tutu* plant during the previous season, one plant was found which not only appeared to be homozygous tunicate, bearing pistillate spikelets in the tassel in profusion, but was also male-fertile. This plant was self-pollinated in the tassel and gave rise in the following generation, which was grown in 1944, to a population of 64 plants, all of which were tunicate. A number of these were self-pollinated and in addition were crossed on various inbred strains, primarily A158 and P39, in order to provide a final test for homozygosity for *Tu*. The crosses thus produced were grown in the season of 1945. Some of these F_1 crosses were so weakly tunicate that they appeared at first glance to be non-tunicate. This weakly tunicate condition was thought at the time to have been the consequence of selection for minus modifiers, but it has since become apparent that the new pod corn involves not only minus modifiers but a new allele of *Tu* which has apparently arisen spontaneously in the course of these experiments. The existence of this allele was first indicated when one of the crosses made to test homozygosity gave rise to strongly tunicate and weakly tunicate plants in a ratio of 8 to 5. The results were verified by repeating a planting of the same cross in 1946 when 10 strongly tunicate and 15 weakly tunicate plants were counted. A third planting in 1947 yielded the two types in a ratio of 8 to 4. The ratio in the total population is 26 strongly tunicate and 24 weakly tunicate. Obviously, the plant selfed in 1944 which furnished the pollen of this cross was either heterozygous for two alleles of *Tu* or was segregating for a major modifier of this gene. The first explanation is now known to be the correct one. Since the weaker form of tunicate produces approximately the same effect when homozygous as does the stronger when heterozygous, it may appropriately be designated as "half-tunicate," and assigned the symbol tu^h . It is illustrated in pl. 47.

Since this cross had been made on the inbred P39 which is pure for sugary, a gene on the fourth chromosome, a further test for allelism was easily made by backcrossing the hybrid to a sugary stock. Plants of two such backcrosses, one with a tunicate hybrid as one parent, the other with a half-tunicate parent, were grown in the summer of 1948 with the following results. The backcross of sugary to the strongly tunicate hybrid yielded four classes in the numbers shown:

Starchy tunicate	32	} 37 crossovers = 38 per cent
Starchy non-tunicate	14	
Sugary tunicate	23	
Sugary non-tunicate	29	

The backcross of sugary to the heterozygous half-tunicate yielded four classes in the following numbers:

Starchy half-tunicate	34	} 28 crossovers = 30 per cent
Starchy non-tunicate	16	
Sugary half-tunicate	12	
Sugary non-tunicate	32	

The results are in harmony with the assumption that the strong and weak forms of tunicate are due to different alleles of *Tu*.

Are There Modern Varieties of Pod Corn?—

Once it was suspected that half-tunicate is an allele of tunicate, the questions at once arose: Are there still weaker alleles of *Tu*? And are there modern varieties of maize which are in reality weak forms of pod corn? An examination of the ears in my collection indicated at once that there are living varieties which give the impression of being weak pod corn. The cobs are flexible and the caryopses are partly covered by membranaceous glumes. In some varieties these glumes are sufficiently developed to almost enclose the seeds, particularly toward the base of the ear where the glumes of pod corn are, as already mentioned, usually most prominent.

The assumption that these types are actually weak forms of pod corn is verified by linkage data. In 1947, for example, there was available in my cultures a population of plants resulting from a cross of a Guatemalan variety, No. 16, with the sweet corn variety, Country Gentleman. The cross had been made to study the linkage relations of pilosity, and the starchy and sugary seeds had been planted separately. When it was discovered that the variety Guatemala 16 appeared to be a weak form of pod corn, a classification of weak-tunicate and non-tunicate was attempted. The difference between them was manifested more strongly in the stiffness and flexibility of the cob than in the glumes themselves. Two classifications, one made by the writer and the other made completely objectively by an assistant who, unaware of the problem involved, merely classified the ears as stiff or flexible, yielded the following results:

	<i>Classified by PCM</i>	<i>Classified by LMJ</i>
Starchy; flexible	18	21
Starchy; stiff	9	6
Sugary; flexible	6	12
Sugary; stiff	25	19
	—————	—————
	58	58

In spite of the discrepancies, there is in both classifications a definite association between starchy endosperm and flexible cobs and sugary endosperm and stiff cobs. If we suppose that flexibility represents one manifestation of a weak form of tunicate, which we may designate as tu^w , then the two middle classes above represent crossovers between Su and tu^w and su and tu . In the first classification these comprise 26 per cent of the total; in the second, 31 per cent. Both figures are remarkably close to the 29 per cent of crossing over which normally occurs between Su and Tu . We have, therefore, a strong indication that the flexibility which is characteristic of the cob of Guatemala No. 16 is actually a weak form of tunicate.

Two additional backcross populations of this type, one involving a Guatemalan and the other a Nicaraguan variety, were grown in 1948. Distinct variation occurred in both populations but was more apparent in the fragility of the cob than in its flexibility, perhaps because the ears had been more completely dried than those grown in 1947. In any case, it was possible to separate the ears into two distinct classes, fragile and solid, on the basis of the ease with which the cobs were snapped in two. The results of such a classification are as follows:

	Family 1583	Family 1585	Total
Starchy; fragile	33	31	64
Starchy; solid	12	15	27
Sugary; fragile	18	12	30
Sugary; solid	25	31	56
	88	89	177

If we assume that fragility of the cob is due to a weak tunicate allele of tu^w then the two middle classes, starchy; solid, and sugary; fragile, represent crossovers. These comprise 32 per cent of the total. Considering the small size of the sample, this is remarkably close to the approximately 29 per cent expected if fragility is the result of a weak allele of Tu .

These combined data strongly indicate that the three varieties involved in these crosses were weak-tunicate and they also indicate that the gene for this condition has its locus on the fourth chromosome approximately 30 crossover units from Su , exactly where an allele of Tu would necessarily have its locus.

Genetic Tests for Alleles of Tu.—

A corollary of the assumption that fertile forms of pod corn can be produced by introducing controlling modifiers from primitive varieties is that the farther removed a variety becomes from its center of origin and its original pod-corn ancestor, the fewer controlling modifiers it will have retained. Hence, if maize originated from a wild pod corn once indigenous to the lowlands of South America, we should expect to find controlling modifiers of pod corn in highest frequency in South American varieties and in lowest frequency in the United States.

To test this assumption, 116 varieties and inbred strains of corn from eight

Latin American countries and from various regions of the United States were crossed on a uniform inbred strain of half-tunicate. The ears of the F_1 hybrids were then studied and classified with respect to the development of the tunicate condition. There was, as expected, considerable variation in the development of the glumes in the F_1 hybrids ranging from those in which the glumes were not visible unless the grains were removed, to those in which the glumes completely covered the seed. The ears were arbitrarily divided into four classes on the basis of a "glume score" defined as follows:

<i>Glume Score</i>	<i>Definition</i>
1	Glumes scarcely apparent.
2	Glumes apparent but do not cover grains.
3	Glumes cover grains on lower part of ear.
4	Glumes cover practically all grains.

When these glume scores were averaged for different countries, and for different areas of the United States (cf. Table I), there proved to be, as had been anticipated, consistent regional differences. But the results were *exactly the reverse* of those predicted. Crosses with South American varieties which were expected to have the lowest glume scores because of controlling modifiers of the tunicate condition had the highest glume score, while varieties from the United States, expected to be highest in glume score, were lowest.

TABLE I

AVERAGE "GLUME SCORES" IN F_1 HYBRIDS OF MAIZE VARIETIES AND INBRED STRAINS WITH AN INBRED STRAIN OF POD CORN

Country, State, or Group	Number of varieties	Glume score
Paraguay	3	3.7
Bolivia	3	3.3
Brazil	2	2.0
Nicaragua	3	3.0
Costa Rica	1	3.0
Mexico	35	2.9
Cuba	3	2.8
Guatemala	6	3.4
Texas	9	2.2
North Carolina	6	2.8
Corn-Belt	17	1.5
Minnesota	10	1.8
Wisconsin	5	2.0
U. S. Sweet Corn Varieties	13	2.1
Av. South America	8	3.1
Av. Central America & West Indies	48	2.9
Av. United States	60	2.0

When an experiment, as in this case, yields results exactly the reverse of those anticipated, it does not mean that the experiment is a failure or that the inductive reasoning which led to it is entirely fallacious. On the contrary, the fact that an experiment yields conclusive results, even if in the "wrong" direction, indicates that the basic premise upon which it rests must have some validity. In this case, the basic premise that South American and North American maize varieties differ in their ultimate relationship to pod corn is undoubtedly valid. But the assumption that this difference is primarily one of modifiers affecting the tunicate conditions is not established. Undoubtedly there are modifiers affecting the tunicate condition; indeed, this fact is easily demonstrated. Perhaps it is even true that controlling modifiers of tunicate have a higher frequency on the average in South American varieties than in North American, but if so, the fact is not established by this particular experiment. What this experiment demonstrates, I think, is that South American and North American varieties of maize differ primarily not in modifiers of tunicate, but in weak alleles of tunicate. When the inbred strain of half-tunicate, tu^h , is crossed with a variety homozygous for weak tunicate, tu^w , then the F_1 , $tu^h tu^w$, might well be expected to have stronger glumes than an F_1 , $tu^h tu$, resulting from a cross with a non-tunicate variety tu .

On this assumption the results in Table I become completely intelligible in terms of the pod-corn hypothesis and are completely in harmony with it. South American varieties have the highest average glume score presumably because weak alleles of Tu have their highest frequency in South America. Central American varieties are intermediate in glume score, and United States varieties lowest. Within the United States the strains of the Corn-Belt proper have lower glume scores than those of any other part of the United States.

The regional differences in glume scores of these F_1 hybrids is strongly correlated with the morphological appearance of the cobs of the parental varieties. The frequency of cobs with "pockets" and the alveolate appearance characteristic of weak pod corn is high in Paraguay, Bolivia, Peru, Ecuador, Colombia¹, Costa Rica, and Guatemala. It is less high in Mexico and the West Indies, and is lowest in the inbred strains of the Corn Belt of the United States. Ears with alveolate cobs from Peru, Colombia, and Mexico are compared with an ear known to be heterozygous for half-tunicate in pl. 48.

The correlation is by no means complete, however, for two varieties which are identical in appearance with respect to the development of glumes may produce quite different hybrids when crossed with tunicate. Furthermore, two varieties whose hybrids with tunicate are identical in glume score may themselves be quite different in appearance. These discrepancies can be attributed to modifier

¹So far as external appearance alone is concerned weak pod corn seems to have its highest frequency in Colombia. This is the only new evidence which I have encountered which supports the conclusion of Birket-Smith (1943) that maize had its origin in Colombia. Cutler (in press) has criticized the linguistic evidence on which Birket-Smith's conclusion is largely based but the evidence from pod corn lends new significance to it. The question of whether maize originated in the Paraguay-Bolivia region or in Colombia is still open but the conclusion that it originated in South America has become almost a certainty.

complexes superimposed upon allelic differences. There is little doubt that both are operating.

But whether the regional differences revealed by this experiment are the result of differences in tunicate alleles, in modifier complexes, or in both, the fact remains that there are consistent differences. This is itself highly significant with respect to the pod-corn hypothesis, for if pod corn is not an ancestral form, if it is simply a mutant which has arisen spontaneously again and again in the history of maize under domestication, then there is no reason why "clines" with respect to genetic factors affecting its expression should exist. The very fact that there are such clines is a strong indication that pod corn has had a role in the evolution of maize.

Additional evidence that both modifiers and alleles of *Tu* are involved in Latin American maize varieties can be obtained by backcrossing to the parental strain of half-tunicate their F_1 hybrids with half-tunicate. If a Latin American variety is *tutu*, then the F_1 hybrid is tu^htu and the backcross to half-tunicate, tu^htu^h , should yield two genotypes, tu^htu^h and tu^htu , in equal numbers. These two genotypes should be readily distinguishable but if modifiers are involved there should be noticeable variation within each class. On the other hand, if a Latin American variety being tested is weak tunicate, tu^wtu^w , then the two classes in the backcross are tu^htu^h and tu^htu^w . These should be less easily distinguishable than the two classes expected in the first instance, and, if modifying factors are also involved, the variation within each class might well result in an overlapping of the two classes to the extent that the two genotypes cannot be accurately separated.

Populations from eight backcrosses have been grown involving two varieties each from Mexico and Nicaragua and four from Guatemala. Four of these yielded two distinct classes with marked variation in each class but with no overlapping. In the remaining four, distinct classes did not occur. There was marked variation in the development of the glumes but it was not possible to separate the ears with complete accuracy into two distinct classes. It seems reasonable to conclude that modifiers of *Tu* were involved in all crosses but that the Latin American varieties entering into the first four crosses were of the genotype *tutu* while in the last four crosses they were tu^wtu^w .

MUTABILITY OF *TU* AND ITS ALLELES

As already mentioned, the weak allele of *Tu* now designated as half-tunicate, tu^h , occurred spontaneously in my cultures involving *Tu*. Since the total number of tunicate plants grown in cultures in which mutations could be detected did not exceed several hundred, it is obvious that *Tu* is either a mutable gene or the sample represented by my cultures is not a random one. Other data are available to indicate that the first explanation is at least in part the correct one.

In the fall of 1946, when harvesting ear-rows of a stock developed originally by crossing pod corn with the Guarany maize of Paraguay and backcrossing repeatedly to the Guarany variety, I discovered one ear heterozygous for *Tu* which was a chimera with respect to the tunicate and non-tunicate condition. Approxi-

mately three-fourths of the ear bore seeds enclosed in glumes while the remainder, comprising one side and the entire tip of the ear, bore naked or partly naked seeds. The ear is illustrated in pl. 45A. Seeds from the two portions were planted separately in 1947 with the results shown below. The ear found in 1946 was open-pollinated so that outcrosses occurred in the progeny. These could, however, be distinguished from plants resulting from selfing or sibbing. The distribution of the progeny from the two portions of the same ear is as follows:

	<i>Outcrosses</i>		<i>Selfs or Sibs</i>		
	<i>Tutu</i>	<i>tutu</i>	<i>TuTu</i>	<i>Tutu</i>	<i>tutu</i>
Tunicate portion	0	3	4	3	1
Non-tunicate portion	0	4	0	2	4

The data, though not extensive, prove that the parent ear was heterozygous for *Tu*, and they strongly indicate that the ear was also a chimera with respect to the two kinds of somatic tissue *Tutu* and *tutu*. The indications are twofold. First, all of the outcrosses, seven in number, proved to be *tutu*. Had the parent ear been of the composition *Tutu* throughout, then the outcrosses should have comprised genotypes *Tutu* and *tutu* in equal numbers. The odds against all being *tutu* are 127:1. Secondly, the distribution of the three genotypes among the selfs and sibs is almost, though not quite, significantly different in the progenies from the two portions of the ear. Both of these facts are in harmony with the assumption that the parent ear was a chimera of *Tutu* and *tutu* tissue, and combined they lend a high degree of plausibility to that assumption. If this is indeed the case, then this represents a second mutation from *Tu*, this time to the allele *tu*, which has occurred in my cultures in the past ten years.

A controlled experiment on mutability involving the allele *tu^h* rather than *Tu* was conducted in 1947 and 1948. Plants of the inbred strain Minn. A158 were crossed by an inbred strain homozygous for two dominant genes, *tu^h* and *B*, the latter a gene responsible for sun-red plant color. Mutations could be readily distinguished in the progeny from the products of accidental contamination by the fact that the latter were recessive for both genes while mutations were recessive for only one. No mutations occurred in the *B* factor in a population of 2125 plants resulting from this cross while one non-tunicate sun-red plant was found. If this proves, on the basis of a progeny test, to be a mutation and not a phenocopy, then the mutation rate at the *tu^h* locus as determined by this single sample is 471 per million gametes. This is only slightly less than the rate, 492 per million, which Stadler found at the *R* locus.

So far as I know, the reverse mutation from *tu* to *Tu* has never been observed. True, tunicate plants for which a spontaneous origin has been assumed have sometimes been discovered in ordinary corn fields. Sturtevant (1894) and Sconce (1912) have both reported the appearance of pod corn in non-podded varieties but the circumstances do not rule out contamination in the previous generation, especially since pod corn has been widely grown as a curiosity. On the other hand, millions of ears of inbred strains and single-crosses have been grown in con-

nection with the production of hybrid seed corn in the past twenty-five years and not a single instance of the spontaneous occurrence of pod corn in these pedigreed cultures has been reported,¹ although other mutations, especially to teopod, have been encountered repeatedly. So far as these data are a criterion, they indicate that *Tu* is not a gene which arose recently through spontaneous mutation but is an ancient gene which has survived in the population perhaps for thousands of generations.

THE APPARENT SPONTANEOUS OCCURRENCE OF SOLITARY TUNICATE SPIKELETS

An interesting phenomenon which must certainly have often been observed, but which so far as I know, has never been reported, is the occurrence of one or more solitary tunicate spikelets or pairs of spikelets on ears which are apparently in all other respects non-tunicate. I have now encountered this phenomenon in three separate instances, in a Nicaraguan variety, in a Mexican variety collected by Dr. E. J. Wellhausen, and in an F_1 hybrid of Midget \times P39. In the last case five different ears each bearing one or more tunicate spikelets were found in a population of 39 ears.

In addition to these three cases, I have received from Dr. Isabel Kelly of Mexico, through the kindness of Dr. Edgar Anderson, a single tunicate kernel found on an ear of Mexican maize. Dr. Kelly writes that kernels of this kind are occasionally found and that they are regarded as having magical properties.

All of these instances of the apparent spontaneous occurrence of tunicate spikelets can, I think, be explained as the monstrous development of glumes on weak forms of pod corn. Certainly this is true of the three ears which I encountered, and since weak pod corn is common in Mexico, I have no doubt that it is true of the case reported by Dr. Kelly. Why an occasional spikelet of weak pod corn should suddenly develop strongly tunicate and even monstrous glumes, and why such spikelets are always basal, is not clear. It is a fact, already mentioned, that the glumes of pod corn are usually more strongly developed on the lower spikelets of the ear than on the upper. It is also a fact that strains of half-tunicate corn sometimes develop monstrous glumes on basal spikelets. But whatever the reason for their occurrence the fact that they do occur is convincing visual evidence that weak forms of pod corn are still truly pod corn.

EVIDENCE OF WEAK POD CORN IN PREHISTORIC TIMES

Many of the prehistoric ears of corn from Peru which I have had an opportunity to examine exhibit the alveolate appearance and the deep "pockets" characteristic of the cobs of weak forms of pod corn. Furthermore, their frequency is highest among the ears from the more ancient sites. Two ears from Tello's Paracas collection are illustrated in pl. 45B, and one from his Nazca collection in pl. 48A. There is little doubt, I think, that all represent weak forms of pod corn.

¹It is possible that ears of pod corn which occur in commercial fields are discarded at processing plants without being reported, but Mr. Ralph Gunn and Mr. R. R. St. John of the DeKalb Agricultural Association have both told me that they have never seen an ear of pod corn in their experimental hybrids. Each has approximately a half-million plants in his tests annually.

A comprehensive study of the prehistoric maize of the Southwest with respect to the presence of weak pod corn has not yet been made. I can only say that many of the ears in the collections of the Peabody Museum of Harvard University have cobs with strongly alveolate surfaces. Also, four ears recently discovered by C. T. Hurst at Cottonwood Cave, Colorado, and sent to me by him for examination have alveolate cobs which closely resemble not only the weak pod corn of modern varieties but also the prehistoric corn of Peru. Dr. Edgar Anderson has kindly given me permission to state here that of twenty-six ears of Basketmaker I corn in the museum at Mesa Verde National Park which were examined by him, eight had prominent glumes. There is little doubt that much, if not most, of the prehistoric corn of both North and South America is weak pod corn.

The facts (1) that the familiar form of pod corn has been found among prehistoric ears; (2) that it, or something curiously like it, is represented in prehistoric ceramic replicas; and (3) that many of the well-preserved ears of prehistoric corn from North and South America are identical in the structure of their glumes and in the alveolate condition of the cobs to modern forms of weak pod corn, represent perhaps the most convincing combination of evidence yet found in support of the pod-corn hypothesis.

THE EARLY EVOLUTION OF MAIZE UNDER DOMESTICATION

The Ancestral Form of Corn.—

In this paper we are concerned only with the early evolution of maize and with the evolutionary paths which it followed before the hypothetical hybridization with *Tripsacum* occurred.

If maize originated from a wild form of pod corn, then we may assume that part or all of the effects now produced by the *Tu* gene contribute toward restoring a primitive or ancestral condition. On the basis of this assumption we can conclude that:

1. Wild corn had its caryopsis enclosed in glumes.
2. The terminal inflorescence bore staminate and pistillate spikelets separately on the same branches, the former below, the latter above, as in *Tripsacum*.
3. Both staminate and pistillate spikelets were paired.
4. The plant bore no "ears" but from the upper nodes arose lateral branches, which, like the main stalk, terminated in a panicle-spike bearing staminate and pistillate spikelets.
5. It is possible, but by no means certain, that the glumes of the pistillate spikelets enclosed two functional florets.

From other evidence we can conclude that:

6. The grains of wild corn were small, flinty, and capable of popping.

There is no way of determining from the evidence (a) whether the plant was an annual or a perennial, or (b) whether branching of the stem was confined to the higher nodes or whether basal branching also occurred. I suspect, largely because there are no perennial forms of maize in existence, that wild corn was an annual.

On the question of basal branching I do not even have grounds for an opinion. Perhaps, as in present-day maize, both high branching and basal branching occurred.

It should be obvious, at least to any student of maize and its relatives, that the plant described above shows a decided resemblance to *Tripsacum*. Indeed, except for its annual habit, its membranaceous glumes, its paired pistillate spikelets, and its central spike, it is virtually identical with *Tripsacum*.

The Change From Wild Pod Corn to Modern Corn.—

If again we assume that wild maize was a form of pod corn, then it is a simple matter to visualize some of the steps involved in its evolution under domestication. Many of the changes which occurred would have been the reverse of those which now occur when the gene *Tu* is superimposed upon a modern variety. On this basis the most important event in the evolution of maize was a mutation in a single gene *Tu*. In the light of the new evidence on *Tu* alleles presented in this paper, we can no longer visualize this as a single drastic change from *Tu* to *tu* (Mangelsdorf and Reeves, 1939). Instead there must have been a series of mutations from higher to lower alleles. In either case, the ultimate effect would have been the same. The glumes became shorter. The lateral branches and their terminal inflorescences became enclosed in overlapping leaf sheaths which largely lost their leaf blades. The lateral inflorescences became pistillate, strongly compacted, and lost their basal branches until only the central spike remained. The terminal inflorescences on the main stalk, the present tassel, became wholly staminate. The caryopsis gradually became larger.

All of those changes initiated by mutations in the *Tu-tu* series which proved to be advantageous to the plant under domestication were accentuated by selection, both natural and artificial, acting upon the genes in the modifier complex so that the ultimate change was considerably greater than that produced by mutations at the *Tu* locus alone.

In following the evolutionary paths which are outlined above, maize has left upon the scene many intermediate forms. This is one important respect in which the pod-corn hypothesis differs significantly from the teosinte hypothesis. If maize originated from teosinte then the intermediate forms which must once have existed are now conspicuously lacking. True, occasional plants are found, as abnormalities, which exhibit the response to short days, characteristic of teosinte, or whose ears are distichous, or whose pistillate spikelets are single; but well-established varieties possessing these teosinte characteristics are unknown. If, on the other hand, maize originated from a wild pod corn then the intermediate forms which must have occurred are still to be found. Intermediate and weak pod forms of tunicate occur not only in prehistoric corn but also in living varieties. Varieties with elongated shanks, prominent leaf blades on the husks, and partly naked ears are common in South America. Varieties breeding true for branched ears are known in both South and Central America. Varieties in which the

development of secondary pistillate florets is the rule rather than the exception are well-known. Individual plants with mixed staminate and pistillate inflorescences are common in many varieties, especially in South America. There is apparently not a single condition intermediate between the hypothetical wild pod corn and modern, highly domesticated corn which does not still exist, usually somewhere in South America. The last fact, incidentally, is of special significance in supporting the hypothesis of a South American origin of maize.

DISCUSSION

Alphonse de Candolle in his classic "Origin of Cultivated Plants" emphasized the importance of utilizing all the evidence which can be brought to bear upon the problem involved in the origin of any particular cultivated plant and pointed out that even a combination of evidence can usually do no more than to lead to a strong probability that any given solution is correct. His conclusions regarding cultivated plants in general are particularly relevant with respect to the problem of the origin of maize, for unless maize should still be discovered actually growing in the wild, a possibility not yet ruled out, the problem of its origin may never be completely and finally solved. It may be possible, however, to accumulate a body of circumstantial evidence bearing upon the problem which will involve probabilities that approach certainty. This point perhaps has not yet been reached. On the other hand, each year of additional research yields new evidence which increases the probabilities that the pod-corn hypothesis is valid and correct and strengthens the view that maize had its origin in South America from a wild form of pod corn. The least that can be said is that the pod-corn hypothesis is no longer merely a plausible alternative to the questionable teosinte hypothesis; it has now become a valid hypothesis in its own right with an impressive body of evidence to support it. The new evidence presented in this paper, that there exists a series of alleles intermediate between *Tu* and *tu*, that intermediate and weak forms of pod corn occurred not only in prehistoric corn, but are common in living varieties of South and Central America, is perhaps the most convincing evidence in support of the pod-corn hypothesis which has yet been brought forward. Considered in the light of the evidence, old and new, summarized in this paper, it appears to me to be conclusive, at least to the extent that the burden of proof now rests upon those who question the pod-corn hypothesis or favor any alternative to it. Indeed, I feel that with the evidence now at hand we can reconstruct the ancestral form of corn with at least as much confidence in the validity of our reconstruction as paleontologists have in their reconstruction of ancestral forms of man, the horse, and other animals.

SUMMARY

1. The *Tu* gene involved in pod corn causes, in appropriate conditions, the development of (a) prominent glumes, (b) pistillate spikelets in the tassel, (c) secondary pistillate florets, (d) branching of the pistillate inflorescence, (e) elongation of the rachis, (f) elongation of the branch supporting the ear.

2. All of these effects contribute to restoring a combination of characteristics probably once primitive.

3. Two spontaneous mutations at the *Tu* locus have occurred in the course of these studies, one from *Tu* to *tu^h*, the other from *Tu* to *tu*. In addition, an experiment on mutability of *tu^h* has yielded one mutation to *tu* in a population of 2125. This corresponds to a mutation rate of 471 per million gametes.

4. A weak form of pod corn called "half-tunicate" resulting from an intermediate allele, *tu^h*, at the *Tu-tu* locus shows 30 per cent of crossing over with *Su* on chromosome 4.

5. Still weaker alleles of *Tu* identified by linkage and other genetic tests are common in living varieties of maize. These have their highest frequency in the maize varieties of South and Central America, and their lowest frequency in inbred strains of the United States Corn-Belt.

6. Much of the prehistoric corn of Peru and some of the prehistoric corn of the American Southwest is identical in appearance to the weak pod corn of present-day Latin American varieties and undoubtedly represents a weak form of pod corn.

7. On the assumption that maize originated from a wild form of pod corn, a reconstructed ancestral form of maize would resemble *Tripsacum* in having lateral branches arising from the nodes of the stem and terminating in panicle-spikes which bear staminate and pistillate spikelets. It would differ from *Tripsacum* in annual habit, in possessing membranaceous rather than indurated glumes, in having a central spike, and in bearing paired pistillate spikelets.

8. Forms intermediate between this hypothetical ancestral form and present-day maize varieties are common in South America.

9. The early stages of the evolution of maize under domestication, those which occurred before *Tripsacum* entered the picture, are now visualized as a series of mutations at the *Tu-tu* locus, each producing numerous morphological changes which, when advantageous under domestication, were accentuated by selection, both artificial and natural, acting upon the modifier complex.

LITERATURE CITED

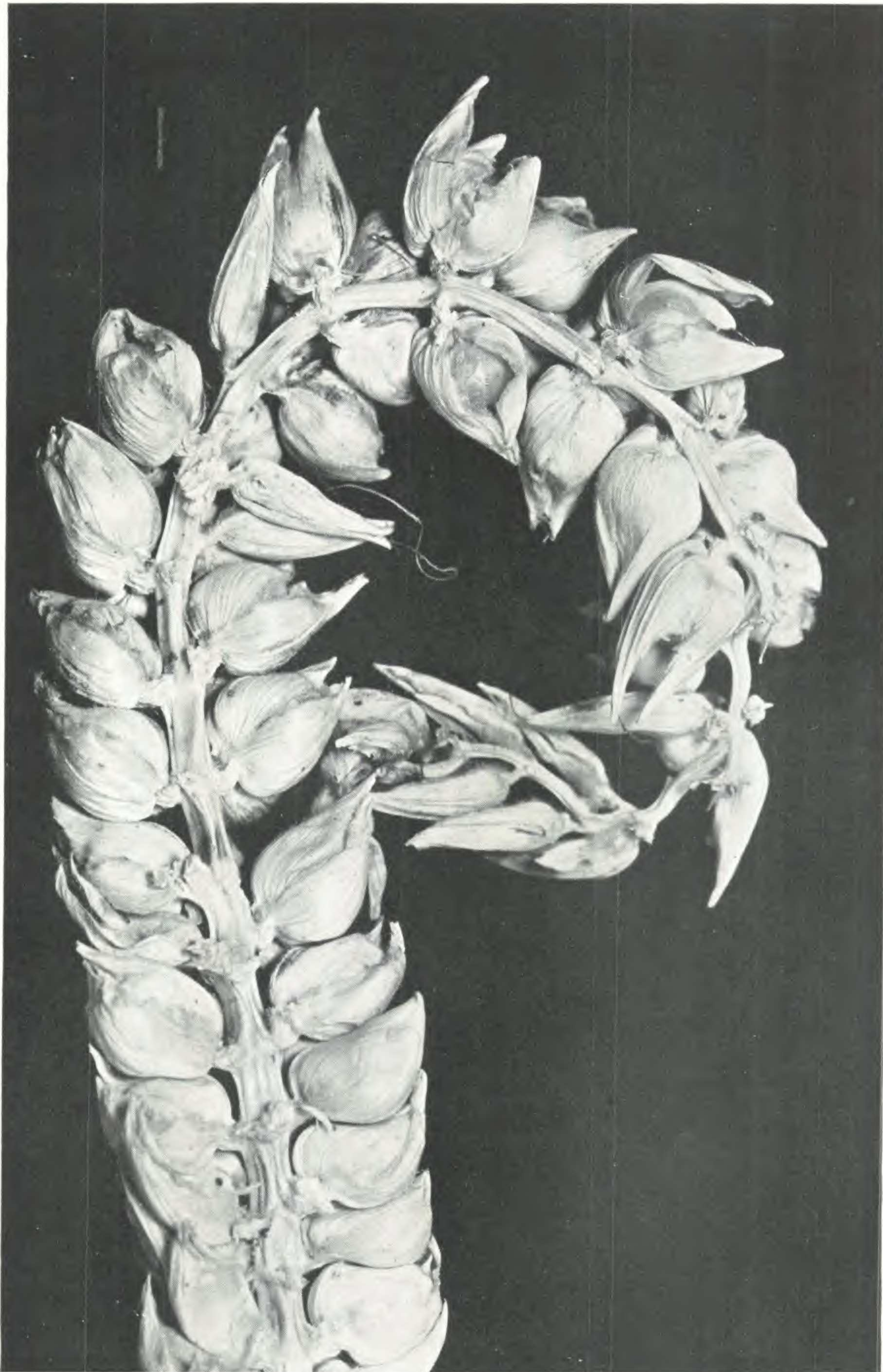
- Azara, F. de (1809). *Voyages dans l'Amérique Méridionale depuis 1781-1801*. 1:146-148. Paris.
- Birket Smith, K. (1943). The origin of maize cultivation. *Kgl. Danske Videnskabernes Selskab, Hist.-Filol. Meddel.* 29³:1-49.
- Bonafous, Matthieu (1836). *Histoire naturelle, agricole et économique du maïs*. Paris.
- Brieger, F. G. (1944). Estudos experimentais sobre a origem do milho. *Anais Escola Sup. Agr. "Luiz de Queiroz"* 1:225-278.
- , (1945). Estudos genéticos sobre o milho Tunicata. *Ibid.* 2:209-238.
- Candolle, A. de (1882). *Origin of cultivated plants*. New York.
- Collins, G. N. (1917). Hybrids of *Zea tunicata* and *Zea ramosa*. *Jour. Agr. Res.* 9:383-396.
- , (1918). Maize, its origin and relationships. *Jour. Wash. Acad. Sci.* 8:42-43.
- Cutler, Hugh C. (1944). Medicine men and the preservation of a relict gene in maize. *Jour. Hered.* 35:291-294.
- , (in press). Geographic origin of maize. *Chronica Botanica* 12:—.
- Dobrizhoffer, Martin (1822). *An account of the Abipones*. London.
- Granado, J. T. del (1931). *Plantas Bolivianas*. La Paz, Bolivia.
- Khankhoje, Pandurang (1930). Nuevas variedades de maiz. *Escuela Nac. Agr., Mexico, Bol. de Invest.* 1.

- Mangelsdorf, P. C. (1945). The origin and nature of the ear of maize. *Harvard Univ. Bot. Mus. Leafl.* 12:33-75.
- , (1947). The origin and evolution of maize. *Advances in Genetics*, pp. 161-207. New York.
- , and R. G. Reeves (1939). The origin of Indian corn and its relatives. *Texas Agr. Exp. Sta. Bull.* 574. 315 pp.
- Parker, A. C. (1910). Iroquois uses of maize and other food plants. *N. Y. State Mus. Bull.* 144.
- Parodi, L. R. (1935). Relaciones de la agricultura prehispanica con la agricultura Argentina actual. *Anales Acad. Nac. Agron. y Vet. de Buenos Aires* 1:115-167.
- Saint-Hilaire, August de (1829). Lettre sur une variété remarquable de Maïs du Brésil. *Ann. Sci. Nat.* 16:143-145.
- Sconce, H. L. (1912). Scientific corn breeding. *Ann. Rept. Amer. Breeders Assoc.* 7:43-50.
- Sturtevant, E. L. (1894). Notes on Maize. *Bul. Torrey Bot. Club* 21:319-343, 503-523.
- , (1899). Varieties of corn. *U. S. Dept. Agr. Off. Exp. Sta. Bul.* 57.
- Weatherwax, P. (1935). The phylogeny of *Zea Mays*. *Amer. Midland Nat.* 16:1-71.

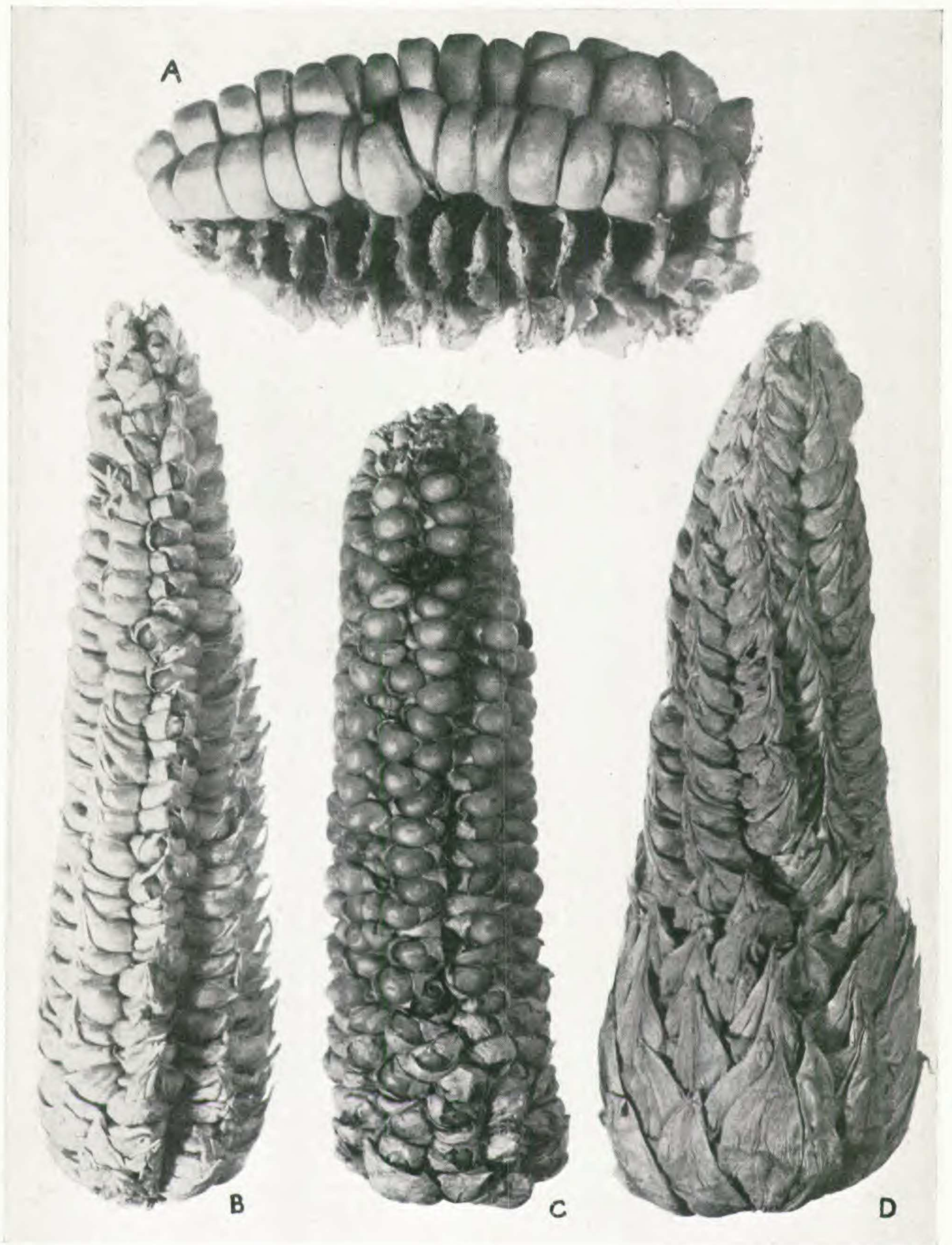
EXPLANATION OF PLATE

PLATE 42

Terminal part of an ear of pod corn produced by crossing the Guarany maize of Paraguay by pod corn and backcrossing repeatedly to the Guarany parent. This ear illustrates several important characteristics of pod corn: (a) the glume-covered caryopsis; (b) the slender and fragile rachis; (c) the lack of compaction.



MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

EXPLANATION OF PLATE

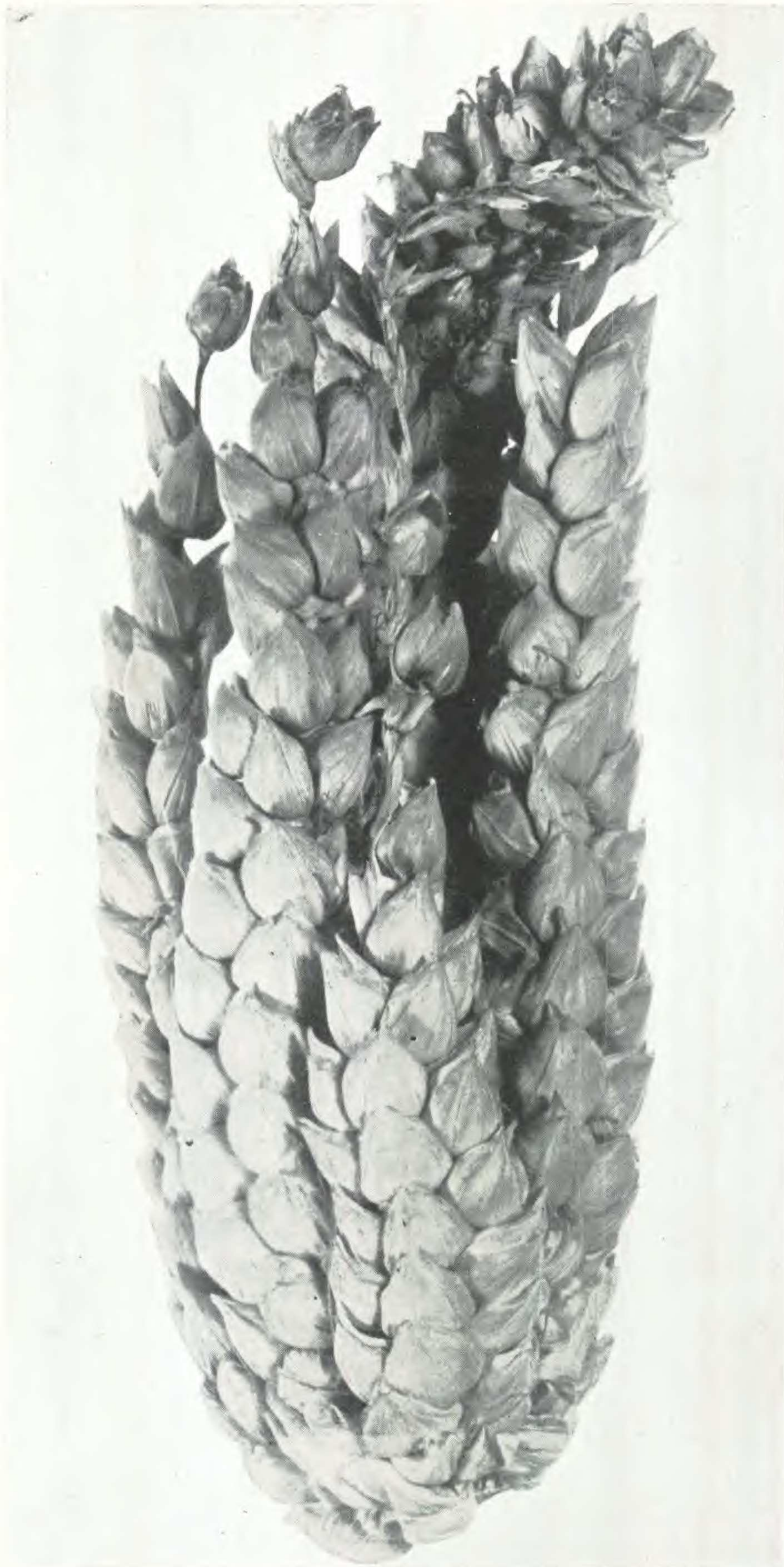
PLATE 43

Pod corn is still well-known in South America. Ears from three countries are illustrated in this photograph. A, Peru. B and C, Bolivia. D, Brazil.

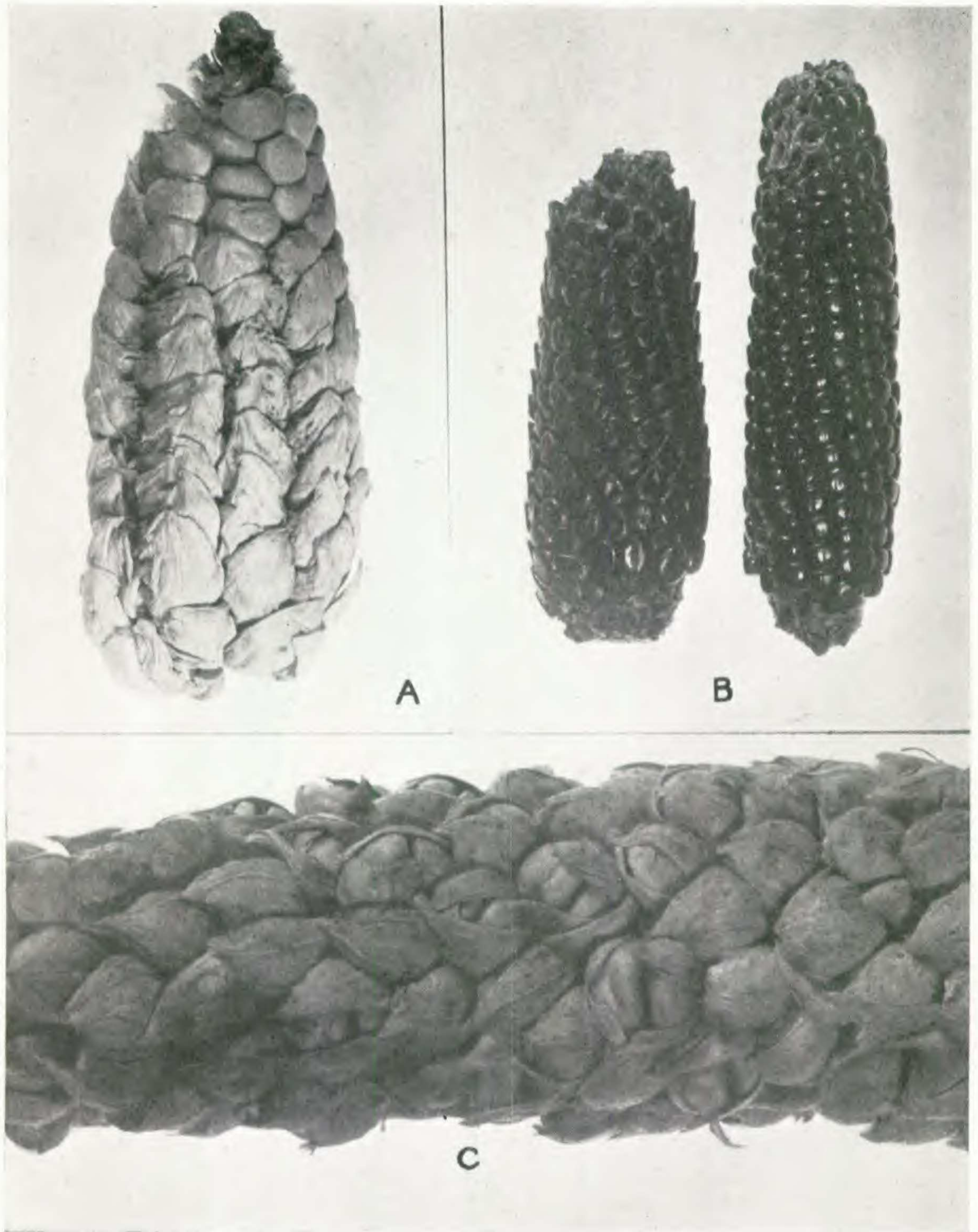
EXPLANATION OF PLATE

PLATE 44

A branched ear of Guarany pod corn. It is not uncommon for ears of pod corn to be branched and this probably represents reversion to a primitive condition.



MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

EXPLANATION OF PLATE

PLATE 45

A. Chimera which represents a mutation from *Tu* to *tu* in somatic tissue. B. Pre-historic ears from Paracas, Peru, showing "pockets" on surface of cob, characteristic of weak pod corn. C. Portion of an ear of Guarany pod corn showing double pistillate florets, possibly a primitive condition.